Vertical distribution of zooplankton in subalpine and alpine lakes: Ultraviolet radiation, fish predation, and the transparency-gradient hypothesis

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Abstract

   The transparency-gradient hypothesis argues that ultraviolet radiation (UV) is a primary determinant of the vertical distribution of zooplankton in transparent lakes with fewer fish, while fish predation is the primary driver in less transparent lakes where fish are more abundant. We measured vertical profiles of UV, photosynthetically active radiation (PAR, essentially visible light used as a proxy for fish predation), temperature, pH, conductivity, chlorophyll *a* (Chl *a*), and zooplankton in seven subalpine and alpine lakes and examined the distribution and abundance of the major zooplankton groups relative to environmental variables using a canonical correspondence analysis (CCA) and multiple regression. Pigment concentrations and UV tolerance of representative species were examined experimentally. The CCA revealed that conductivity, PAR, and UV were most related to zooplankton distribution and abundance. The cladoceran *Daphnia* was associated with high PAR, while cyclopoids and nauplii were associated with low PAR. In contrast, the vertical distribution of calanoids was positively related to UV, while *Holopedium* was negatively associated with UV. The regressions revealed that UV consistently explained more of the variance in zooplankton vertical distribution than did either PAR or chlorophyll. Calanoids had high concentrations of photoprotective compounds and a relatively high UV tolerance compared to *Daphnia*. The positive association of *Daphnia* with visible light (PAR) and the importance of UV in overall zooplankton vertical distribution support the transparency-gradient hypothesis, indicating that UV is more important than fish predation in controlling the vertical distribution of zooplankton in more transparent lakes.

The vertical distribution of zooplankton is mediated by a wide array of environmental factors, including abiotic factors such as light and temperature, as well as biotic factors such as food and predators (Lampert 1989). The relative importance of these various factors is likely to vary among lakes as well as among zooplankton species and even clones within a single species. There are also strong interactions among environmental factors. For example, the response of *Daphnia* to variation in food concentrations in the water column is modified by temperature gradients (Kessler and Lampert 2004; Winder et al. 2004). The relative importance of behavioral vs. pigmentation responses may also vary with taxon and latitude of a given zooplankton population (Hansson et al. 2007). Similarly, chemical kairomones released by fish stimulate stronger

negative phototaxis in *Daphnia* collected from lakes with high fish predation pressures than in *Daphnia* collected from lakes with low predation pressures (De Meester 1993). An in situ experimental study similarly demonstrated a stronger negative phototaxis to solar ultraviolet (UV) radiation in a highly transparent lake than in a low transparency lake (Leech et al. 2005*a*). This has led to the hypothesis that fish predation is more important in stimulating downward migration of zooplankton in less transparent lakes, while UV is more important in highly transparent lakes where fish populations are low (Leech et al. 2005*a*). Here, we refer to this as the ''transparency-gradient'' hypothesis.

   Alpine lakes are an extreme habitat where zooplankton must cope with very low average temperatures, low concentrations of food, and high fluxes of solar UV radiation (Sommaruga 2001). These factors combine to form vertical habitat gradients in alpine lakes that influence the vertical distribution of zooplankton (Winder et al. 2004). The high flux of solar radiation inhibits primary productivity near the surface of those lakes and may cause the maximal phytoplankton abundance to be located in deeper strata (Sommaruga 2001), resulting in the development of a deep-water chlorophyll maximum (DCM). The combination of high UV exposure, a DCM with a steep temperature gradient, and cold hypolimnetic temperatures in alpine lakes is thus likely to have an unusually strong influence on the vertical distribution of zooplankton. Visual predators such as fish are widely recognized as important determinant of the vertical distribution of

zooplankton in more productive low-elevation lakes (Lampert 1989). In alpine lakes, which are characteristically fishless, the stocking of fish may lead to the elimination of large zooplankton species (McNaught et al. 1999; Parker and Schindler 2006), but, consistent with the transparency-gradient hypothesis, data to date suggest that fish have little or no effect on zooplankton vertical distribution in these low-productivity systems, even when fish are stocked (Winder et al. 2004).

Experimental studies have demonstrated the potential role of UV radiation in determining the vertical distribution of zooplankton. Laboratory experiments have demonstrated that *Daphnia magna* are negatively phototactic to UV and positively phototactic to longer wavelengths of visible light (Storz and Paul 1998). Laboratory and outdoor experiments in 1-m-deep mesocosms demonstrated a deeper depth distribution of *Daphnia* spp. in the presence of UV vs. in its absence (Rhode et al. 2001). In situ experiments that manipulated UV in 2.2-m-long columns confirmed the avoidance of UV by *Daphnia* and, to a lesser extent, by copepods (Leech and Williamson 2001; Leech et al. 2005*a*). Other experiments in these in situ columns demonstrated that the presence of the invertebrate predator *Chaoborus* modified the depth distribution of *Daphnia* relative to UV (Boeing et al. 2004). Interestingly, *Chaoborus* itself appears to migrate deeper in response to visible light but does not respond to UV (Persaud et al. 2003). Larger-scale in situ experiments in 8-m-deep mesocosms further confirmed that UV avoidance in *Daphnia* was greater than that of Diaptomid copepods (Fischer et al. 2006).

Survey data also support the importance of UV in the vertical distribution of zooplankton. For example, in two different studies in North and South America, each of which looked at three lakes, the avoidance of the surface by zooplankton was stronger in high-UV lakes than in low-UV lakes (Alonso et al. 2004; Leech et al. 2005*b*). The fact that zooplankton are negatively phototactic to UV and positively phototactic to visible light also suggests that UV may be central to the positive relationship observed between the migration amplitude of zooplankton and Secchi transparency (Dodson 1990; Winder et al. 2004). Perhaps some of the most convincing evidence for the importance of UV in regulating the vertical distribution of zooplankton is the avoidance of surface waters during the day by zooplankton that show diel vertical migrations in fishless lakes (Hairston 1980; Williamson et al. 2001*b*; Aguilera et al. 2006).

In spite of the compelling evidence for the importance of UV in zooplankton vertical distribution, there are no systematic studies of the importance of UV relative to other environmental factors in alpine lakes. It is also unknown whether vertical distribution responses to high UV in alpine lakes vary among zooplankton taxa. The importance of UV to zooplankton vertical distribution is still an open question because zooplankton have evolved a whole array of defense mechanisms against UV radiation that increase their UV tolerance (Siebeck et al. 1994; Zagarese and Williamson 1994) and may let them persist in warmer surface waters where there may be a demographic advantage. Zooplankton can accumulate photoprotective compounds such as carot-enoids and mycosporine-like amino acids (MAAs) (Tartarotti et al. 2001; Persaud et al. 2007) that either directly protect their deoxyribonucleic acid (DNA) from damaging UV radiation or quench UV-generated reactive oxygen species. Small-scale laboratory experiments have demonstrated the reduced behavioral response of pigmented vs. unpigmented zooplankton to UV (Rhode et al. 2001). Enzyme-driven processes, including light-dependent photoenzymatic repair (PER) and light-independent nucleotide excision repair (NER), can also repair DNA damage caused by UV radiation (MacFadyen et al. 2004; Häder and Sinha 2005), but the extent to which these defenses are utilized varies among zooplankton groups.

Here we use two separate analyses to assess (1) the potential importance of UV radiation relative to a suite of other environmental variables in regulating the abundance of zooplankton across a gradient of subalpine to alpine lakes, and (2) the relationship of variation in food concentration, UV transparency, and visible (PAR) transparency to the vertical distribution of zooplankton within these same lakes. We also examined the UV tolerance and pigment concentrations of representatives of the two dominant crustacean zooplankton taxa. Our objective was to extend prior experimental work to examine the extent to which the observed vertical distribution patterns of the major zooplankton taxa are consistent with a UV avoidance hypothesis and, more broadly, the transparency-gradient hypothesis. Separating the effects of fish predation from UV avoidance in situ is a notoriously difficult problem, and no prior studies of fish predation have simultaneously examined the potential role of UV radiation. This is a concern because the presence of planktivorous fish can have a strong effect on water transparency (Mazumder et al. 1990; Parker and Schindler 2006). In our study lakes, UV and PAR transparency showed different patterns among lakes (*see* Results). Thus, we were able to run regressions of variation in zooplankton vertical distribution (as the dependent variable) separately with respect to variation in both UV transparency and PAR transparency among lakes to assess whether variation in the vertical distribution of zooplankton among lakes was more consistent with a UV avoidance hypothesis or a fish predation avoidance hypothesis.

Methods

Study lakes and sampling—The seven study lakes are situated at elevations ranging from 2460 to 3162 m in the Beartooth Absaroka Wilderness at the boundary of the states of Montana and Wyoming (Saros et al. 2005). They differ in their UV transparency but have similar thermal stratification patterns (Table 1). In August 2003, we measured the attenuation of ultraviolet radiation at 320 nm ($UV_{320 nm}$) and 380 nm ($UV_{380 nm}$), and photosynthetically active radiation (PAR, 400–700 nm) wavelengths were measured using a Biospherical Instruments Cosine (BIC) submersible radiometer (Biospherical Instruments), a medium bandwidth submersible radiometer that measures photosynthetically active radiation as well as UV in three wavelength bands (305, 320, and 380 nm) with a depth

Table 1.   Averages (±1 SD) of conductivity (Cond), pH, Chl *a*, and zooplankton abundance in all seven lakes. Da, *Daphnia*; Ho, *Holopedium*; Ca, calanoid copepods; Cy, cyclopoid copepods; and Na, nauplii. Also, the depths of 1% of surface irradiance for 320 nm UV ($Z_{1\%UV320\ nm}$) and 10% PAR ($Z_{10\%PAR}$), the depths of the deep-water chlorophyll maximum ($Z_{Chl\ a}$), and depths of maximal abundance of the respective zooplankton groups are shown.

Lake	Kersey	Island	Beartooth	Heart	Beauty	Emerald	Fossil
Elevation (m)	2460	2901	2713	3162	2874	2991	3018
Max. depth (m)	20.7	30.5	26.2	45.7	35.1	50.0	45.7
Cond (μS cm^{-1})	14.9±0.9	6.5±0.6	33.3±3.2	8.1±1.5	7.0±0.9	7.0±0.7	2.2±0.4
pH	7.6±0.5	7.3±0.3	7.9±0.2	9.0±0.7	8.0±0.2	8.4±0.8	7.6±0.2
Chl *a* (μg L^{-1})	2.1±0.9	2.4±1.2	1.6±0.6	9.5±4.0	1.2±0.3	2.5±1.6	1.2±0.5
Da (ind. L^{-1})	2.0±1.6	1.0±0.9	2.0±1.6	1.4±2.4	3.2±3.4	6.2±5.9	0.7±1.5
Ho. (ind. L^{-1})	0.7±1.0	2.4±0.5	0.7±1.0	0±0	6.8±6.3	0±0	7.5±5.7
Ca (ind. L^{-1})	0.2±0.2	6.9±6.4	0.2±0.2	0±0	0.2±0.1	2.5±1.6	3.5±2.2
Cy (ind. L^{-1})	4.4±9.1	1.5±2.0	4.4±9.1	0.3±0.4	0.6±0.5	0.2±0.2	0.2±0.2
Na (ind. L^{-1})	2.0±3.5	23.2±25.6	2.0±3.5	6.6±9.9	5.5±5.1	2.2±3.4	1.5±0.8
$Z_{1\%UV320}$ (m)	0.6	1.2	1.4	2.5	2.5	4.3	6.7
$Z_{1\%PAR}$ (m)	10.0	12.6	12.8	10.0	>17	19.0	>25.0
$Z_{10\%PAR}$ (m)	5.0	6.1	6.6	4.9	9.4	8.6	12.9
$Z_{Chl\ a}$ (m)	10.5	12	12	11	15	14	18
Z_{Da} (m)	3	3	3	5	3	10	18
Z_{Ho} (m)	1	3	1	–	3	–	15
Z_{Ca} (m)	6	15	6	–	3	10	6
Z_{Cy} (m)	6	6	6	11	12	14.5	18
Z_{Na} (m)	6	9	6	11	6	18	15

resolution of 0.01 m. The ultraviolet radiation (UVR) bands have a bandwidth of 8–10 nm measured as the full width at half maximum response (FWHM = the range between the two wavelengths at which response is 50% of the peak response). The BIC has a deck cell that simultaneously records the same UVR and PAR wavelengths as the submersible cell in order to account for short-term changes in atmospheric conditions (clouds, aerosols, etc.). UV and PAR attenuation depths ($Z_{1\%}$) are measured values that give the depth (m) at which UV of a given wavelength is 1% of subsurface irradiance. Thus, albedo and variation due to clouds, aerosols, and surface waves are not included in these values, and the value of UV or PAR is dependent only on water transparency. Where optical properties of water are constant over depth, the diffuse attenuation coefficients (K_d) and 1% attenuation depths ($Z_{1\%}$) for a given wavelength can be modeled as the negative slope of the relationship between the natural log of irradiance (E) vs. depth (Z, in units of m) based on the following equations:

$$K_d = \frac{\ln\left(\frac{E_0}{E_z}\right)}{Z} \tag{1}$$

$$Z_{1\%} = \frac{4.605}{K_d} \tag{2}$$

Water temperature, pH, and conductivity were measured at 1-m depth intervals from the surface to the hypolimnion using a Hydrolab multiparameter probe (Hach Environmental). Chl *a* was sampled at six different depths in each lake by collecting and filtering 1.0–1.5 liters of lake water through a Whatman GF/F filter for each sample depth. Filters were placed in petri dishes, wrapped in foil, and stored in a freezer. Chlorophyll was extracted in 90%

acetone, and the extract was clarified by centrifugation. Chl *a* concentrations were determined spectrophotometrically according to standard methods (APHA 1989). All samples were analyzed within three weeks of collection.

Zooplankton were sampled at midday (within 3 h of solar noon) at six to seven different depths using a 2- or 3-liter Van Dorn bottle. Two bottles were pooled for each replicate, and three replicates were taken at each depth. The sampling depths were selected with the goal of capturing data from the epilimnion to the depth of the DCM in increments of 2, 3, or 4 m. The samples obtained with the Van Dorn bottles were concentrated on a 48-μm mesh, transferred into scintillation vials, and fixed in 70% ethanol. Zooplankton were counted in a Bogorov chamber under a dissecting microscope at 10×–30× magnification. Individuals were categorized into calanoid copepods, cyclopoid copepods, *Daphnia*, *Holopedium*, and copepod nauplii. The calanoids were all in the family Diaptomidae, and included *Leptodiaptomus tyrelli* in Kersey Lake, *Leptodiaptomus ashlandi* in Beartooth Lake, *Aglaodiaptomus lintoni* in Beauty Lake, and *Arctodiaptomus arapahoensis* in Emerald and Fossil Lakes. The cyclopoid copepods were all in the family Cyclopidae and included *Acanthocyclops vernalis* and *Orthocyclops modestus* in Kersey Lake, *A. robustus* in Beauty Lake, *Diacyclops thomasi* in Beartooth and Island Lakes, and *A. vernalis* in Heart Lake. No adult female specimens were available for positive species identification of the cyclopoid in Fossil Lake. Copepod nauplii included both calanoids and cyclopoids combined. These lakes all contain stocked salmonids, including brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), and cutthroat trout (*Oncorhynchus clarki*).

Measurement of photoenzymatic repair and pigment analysis—In addition to the vertical profiles taken in

August 2003, we sampled the calanoid copepod *Leptodiaptomus ashlandi* from Beartooth Lake and *Daphnia pulicaria* from Emerald Lake in July 2004. All *D. pulicaria* in Emerald Lake were pale, whereas all *L. ashlandi* in Beartooth Lake were red. We measured the concentration of mycosporine-like amino acids and carotenoids as well as their UV tolerance. These lakes and species were chosen for the abundance and availability of representatives of the two major crustacean groups in the lakes. For both purposes, *L. ashlandi* and *D. pulicaria* were sampled with a 243-μm net. About 20 tows were taken from 15-m and 30-m depth to the surface, respectively. Both *L. ashlandi* and *D. pulicaria* specimens were isolated from the zooplankton tows the same day that they were sampled and prepared for either the pigment analysis or the experiment on UV tolerance.

Measurements of mycosporine-like amino acids (MAAs) and carotenoids—We measured MAAs and carotenoid concentrations of adult *L. ashlandi* from Beartooth Lake and juvenile *D. pulicaria* from Emerald Lake following the methods described in Moeller et al. (2005). We isolated *D. pulicaria* and egg-bearing *L. ashlandi* from the samples and removed the egg clutches from the *L. ashlandi*. For the MAA analysis, we mounted two replicates each with 50 *L. ashlandi* females and 30 *D. pulicaria* specimens on preweighed glass slides and froze them at $-20°C$ until further analysis. The samples were freeze dried, weighed on a Cahn electrobalance to the nearest microgram, sonicated in 0.75 to 1.5 mL 25% aqueous methanol, extracted over 24 h, and subjected to high-performance liquid chromatography (HPLC) in a Shimadzu LC-10AD/SCL-10A chromatograph. The detector was a stop-flow scanning photometric detector (SPD-10AV), which records absorbance at 313 and 340 nm. The stationary phase consisted of a Brownlee RP8 column (Spheri 5, 250×4.6 mm). The mobile phase consisted of 25% aqueous methanol with 0.1% acetic acid run at a flow rate of 0.8 mL min^{-1}. Copepods from Lake Giles (Pike County) served as a standard (Moeller et al. 2005). The system was calibrated against porphyra-334 from a concentrated extract of *Porphyra tenera*.

For the carotenoid analysis, 70 and 54 adult *L. tyrelli* females and 5 and 14 *D. pulicaria* individuals were suspended in four vials containing 2 mL of 100% ethanol each. These vials were stored at $-20°C$ until they were analyzed. The vials were thawed at $8°C$ for 24 h before the analysis. The spectrophotometric absorbance of the extracts was measured in a spectrophotometer (Shimadzu RF-551) at 474 nm (absorption maximum of carotenoid) and related to the dry weights. Dry weights were measured prior to the MAA analysis to permit estimation of carotenoid concentrations (mg dry weight)$^{-1}$ (Persaud et al. 2007).

Measurement of UV tolerance and photoenzymatic repair—The UV tolerance of both *Daphnia* and *Leptodiaptomus* in the presence and absence of photorepair radiation (PRR, consisting of visible light and UVA radiation required for photoenzymatic repair of UV-induced DNA damage) was quantified with a UV lamp phototron

(Williamson et al. 2001*a*). This instrument provides the amount of UV damage in 12 h equivalent to that experienced during a single day of natural solar radiation exposure in the surface waters of a clear lake at 40°N latitude when taking into account both incident UV irradiance and the biological weighting function for *Daphnia* (Williamson et al. 2001*a*). Two experiments were performed, one with egg-bearing *L. ashlandi* and one with juvenile *D. pulicaria*. On the day before each of the experiments, 10 individuals of either egg-bearing *L. ashlandi* or juvenile *D. pulicaria* were randomly distributed in each of 45 quartz dishes. *L. ashlandi* and *D. pulicaria* were exposed to UV radiation for 12 h at $17 \pm 1°C$ with UV irradiances of 16, 28, 36, and 58 kJ m^{-2} for *L. ashlandi* and 5, 16, 28, and 36 kJ m^{-2} for *D. pulicaria*. We chose different UV irradiances because copepods tend to be more UV tolerant than *Daphnia* (Leech and Williamson 2000). Zooplankton in 20 dishes received photorepair radiation during the UV exposure, whereas zooplankton in 20 other dishes did not. All treatments (irradiance level $\times$ photorepair radiation) were replicated five times. Additionally, zooplankton in five dishes that were not exposed to light served as dark controls.

The dishes containing *L. ashlandi* were examined for survival for 5 d after the exposure period. The survival of *D. pulicaria* could only be followed for 3 d after the exposure due to the mortality in the dark controls exceeding 10% after 3 d. As a measurement of UV tolerance, we compared the UV exposure levels (irradiance) that caused 50% mortality (LE$_{50}$) in the respective species after being corrected for mortality (always <10%) in the dark controls.

Statistical analysis—Comparison of distribution and abundance among lakes: Zooplankton distribution patterns among lakes were explored with respect to a suite of environmental variables across seven lakes using canonical correspondence analysis (CCA). These parameters included PAR, UV$_{380 \text{ nm}}$, UV$_{320 \text{ nm}}$, temperature, pH, conductivity, and chlorophyll concentration, which were measured at the same depths at which the zooplankton were sampled. All light parameters were expressed as a percent of the surface irradiance. Temperature, conductivity, and chlorophyll were log transformed, and zooplankton abundances were square-root transformed to meet assumptions of normality in data distribution. As multiple depths were sampled within each of the seven lakes, data were blocked by lake in the analysis by treating lakes as covariables. Forward selection with Monte Carlo permutation tests restricted within blocks was used to determine the significance of each environmental variable in influencing species composition; only variables that were significant ($p < 0.05$) were included in the model. Ordination analyses with biplot scaling were performed with Canoco version 4.5 (Ter Braak and Smilauer 2002).

Vertical habitat selection within lakes: In order to assess the relative importance of food and UVR in the vertical habitat selection of zooplankton, we performed a stepwise multiple regression analysis with backward selection using SPSS 11.5 for Windows (SPSS). The predictors were the

depths of the maximum Chl *a* concentration and the depths at which 1% of the surface irradiance of $UV_{320\,nm}$ ($Z_{1\%UV320\,nm}$) or 10% of the surface irradiance of PAR ($Z_{10\%PAR}$) were measured. We ran separate regressions for $UV_{320\,nm}$ and PAR to assess the relative responses to UV damage (driven by $UV_{320\,nm}$) vs. fish predation (driven by PAR). The dependent variable was the depth of maximal abundance of each zooplankton group in the seven lakes. In order to assess the influence of water transparency on the temperature regime to which zooplankton were exposed, we ran linear regressions using (1) the depths of maximum abundance and (2) the temperatures at the depths of maximum abundance of the different zooplankton groups as the response variables. The predictors were $Z_{1\%UV320\,nm}$ and $Z_{10\%PAR}$, respectively.

Measurement of UV tolerance and photoenzymatic repair: A two-way ANOVA was used to test for the significance of the effects of damaging UV and photoenzymatic repair on survival using arcsine square-root-transformed survival data, where UV exposure level and the presence or absence of photorepair radiation were the two factors. The UV exposure level that reduced survival to 50% (LE_{50}) was estimated through linear regression of logit-transformed survival data vs. UV exposure level.

Results

Among-lake patterns—The conductivity in the study lakes ranged from 2.2 to 33.3 μS cm^{-1}, and the pH ranged from 7.3 to 9 (Table 1). The seven lakes were similar in the depth of their surface mixed layer (4–5 m), although the maximum temperatures varied as much as 5°C among lakes (Fig. 1A). All lakes contained a deep chlorophyll maximum (DCM) (Fig. 1B). Average Chl *a* concentrations were low (1.6–2.5 μg L^{-1}), except in Heart Lake, which had an average of 9.5 μg L^{-1} (Table 1). The UV transparency ($Z_{1\%320\,nm}$, depth to which 1% of surface 320 nm UV penetrated) varied 10-fold, from 0.6 m in Kersey Lake to 6.7 m in Fossil Lake (Table 1; Fig. 1C). The range of transparency to PAR ($Z_{10\%PAR} = 5.0$–12.9 m) was less variable than that for UV and showed a different pattern than UV across lakes (Fig. 1C). For example, the PAR transparency of Kersey and Island Lakes was fairly similar ($Z_{10\%PAR} = 5.0$ and 6.1 m, respectively), while the UV transparency differed by a factor of two ($Z_{1\%320\,nm} = 0.6$ and 1.2 m, respectively). On the other hand, the UV transparency of Heart and Beauty Lakes was identical ($Z_{1\%320\,nm} = 5.0$ m), but their PAR transparency differed by almost 2-fold ($Z_{10\%PAR} = 4.9$ and 9.4 m, respectively) (Table 1; Fig. 1C).

The CCA revealed that 27.5% of the variance in the zooplankton data was explained by the measured environmental variables (Fig. 2). Forward selection revealed that the variances in zooplankton distribution and abundance explained by conductivity, %PAR, and $\%UV_{320\,nm}$ were all significant ($p < 0.05$). The remaining variables were removed from the CCA by forward selection because they either co-varied with selected parameters or they explained only a small percentage of the total variance and were not significant. With the three selected variables, the first axis
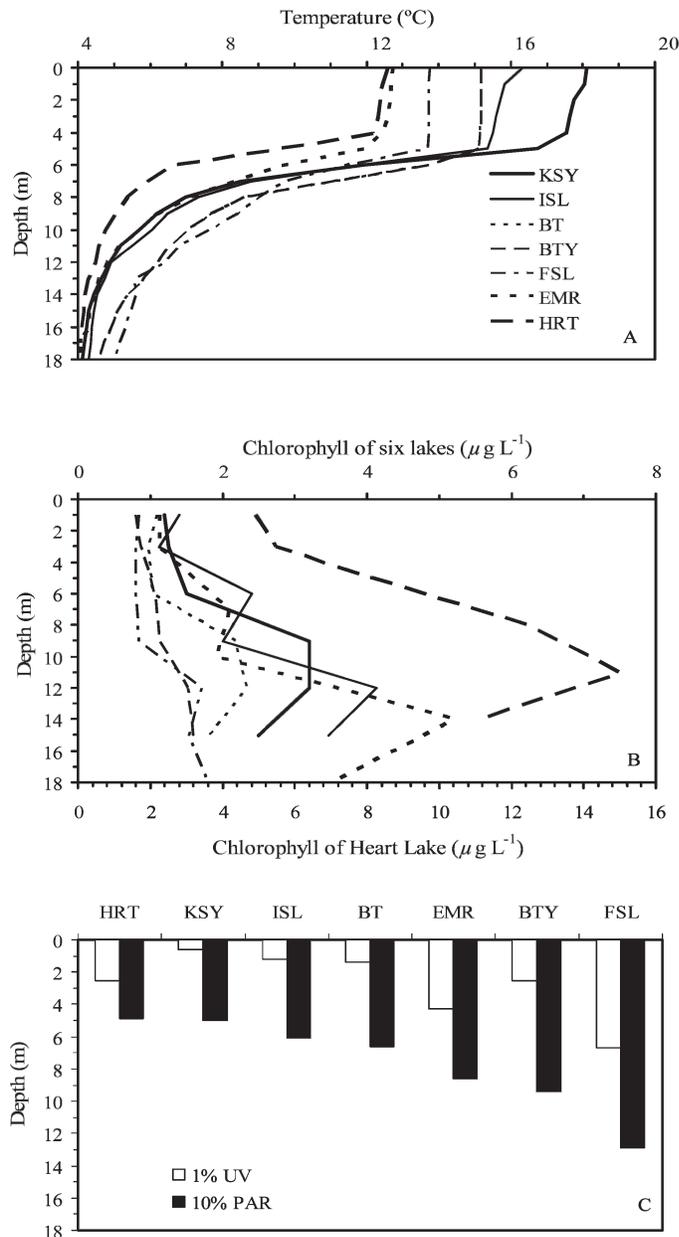

Fig. 1. (A) Temperature, (B) Chl *a* profiles, and (C) 1% 320 nm and 10% PAR depths of the seven study lakes. Chl *a* concentrations for Heart Lake are shown on the bottom axis; concentrations for the other six lakes are on the top axis. KSY = Kersey, ISL = Island, BT = Beartooth, BTY = Beauty, FSL = Fossil, EMR = Emerald, and HRT = Heart.

explained 53% of the total explained variance and was correlated with conductivity (0.45) and %PAR (0.40). The second axis accounted for an additional 38% of the total explained variance and was correlated with $\%UV_{320\,nm}$ (0.59). Across the seven lakes, *Daphnia* individuals were consistently present in samples with high %PAR and conductivity, whereas the opposite was found for cyclopoid copepods and nauplii (Fig. 2). Calanoid copepods were more abundant at higher $UV_{320\,nm}$ and PAR levels, whereas *Holopedium* was abundant in samples with low $\%UV_{320\,nm}$ levels.
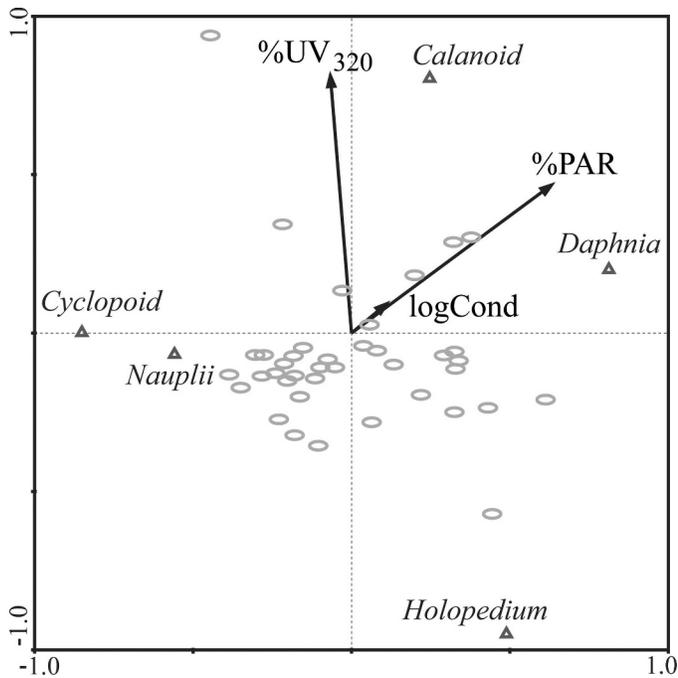
Fig. 2. Canonical correspondence analysis (CCA) ordination diagram, showing the association of the different zooplankton groups (marked with a triangle) with conductivity (logCond), and both PAR and $UV_{320\ nm}$ irradiance. The placement of all samples used in the analysis (ovals) is also indicated. The vectors show the direction of maximum variation of the given variable across the diagram.

Vertical distribution patterns—The depths of the maximum abundance of *Daphnia*, *Holopedium*, cyclopoid copepods, and nauplii all increased significantly with increases in either chlorophyll or some metric of water transparency or both (Tables 1, 2). UV transparency consistently explained more of the variance in vertical distribution of each of these groups than did either PAR or chlorophyll. For *Daphnia*, *Holopedium*, and cyclopoid copepods, the R^2 values for chlorophyll and PAR ranged from 0.66 to 0.81, while those for UV ranged from 0.92 to 0.95 (Table 2). Neither chlorophyll nor PAR explained a significant proportion of the variance in vertical distribution of nauplii ($R^2 \leq 0.25$; Table 2). In contrast to these other zooplankton groups, the depth of the calanoid copepod maximum was not significantly related to either water transparency or the depth of the Chl *a* maximum (Tables 1, 2). Least-squares linear regressions using water transparency to $UV_{320\ nm}$ ($Z_{1\%UV320\ nm}$) and PAR ($Z_{10\%PAR}$) as predictors and temperature at depth of maximal abundance of each zooplankton group as the dependent variable revealed that the deeper depth distributions of *Daphnia* and *Holopedium* in the more UV transparent lakes (Tables 1, 2) exposed these groups to significantly lower temperatures ($R^2 = 0.83$ and 0.97; $p = 0.005$ and 0.002, respectively, for these two species). This relationship between depth of peak abundance and temperature was not significant for calanoids, cyclopoids, or nauplii ($R^2 = 0.01$, 0.55, and 0.31; $p = 0.88$, 0.056, and 0.198, respectively). The relationship between PAR transparency and temperature

Table 2. Results of stepwise multiple regressions (backward selection) using the depth of the DCM ($Z_{Chl\ a}$) and 1% of surface irradiance of $UV_{320\ nm}$ ($Z_{1\%UV320\ nm}$) as single and dual predictors and using $Z_{Chl\ a}$ and 10% of surface irradiance of PAR ($Z_{10\%PAR}$) as single and dual predictors. The dependent variables were the depths of maximal abundance of five zooplankton taxa. Italic values are significant ($p < 0.05$).

Species	R^2			R^2		
	$Z_{Chl\ a}$	$Z_{1\%UV320\ nm}$	Both	$Z_{Chl\ a}$	$Z_{10\%PAR}$	Both
Daphnia	*0.65*	*0.92*	*0.93*	*0.65*	*0.66*	*0.66*
Holopedium	*0.79*	*0.95*	*0.97*	*0.79*	*0.81*	*0.82*
Calanoids	0.09	0.02	0.20	0.09	0.11	0.30
Cyclopoids	*0.70*	*0.92*	*0.92*	*0.70*	*0.68*	*0.72*
Nauplii	0.25	*0.63*	*0.81*	0.25	0.24	0.25

was not significant for most groups ($R^2 = 0.03$–0.38; $p > 0.143$). The exception was *Holopedium*, which was associated with colder temperatures in the lakes that were more transparent to PAR ($R^2 = 0.86$; $p = 0.023$).

UV tolerance experiments—The increased survival of both *Leptodiaptomus* and *Daphnia* in the presence of photorepair radiation indicates the importance of photoenzymatic repair as a UV defense mechanism in these two species (Fig. 3; two-way ANOVA, effects for photorepair radiation: *Daphnia* $F_{1,39} = 295$, $p < 0.001$; *Leptodiaptomus* $F_{1,39} = 66$, $p < 0.001$). The UV exposure level that is lethal for 50% of the individuals (LE_{50}) for *Leptodiaptomus* was 54 kJ m^{-2} when they were also exposed to photorepair radiation. In the absence of photorepair radiation, *Leptodiaptomus* was much less tolerant ($LE_{50} = 17$ kJ m^{-2}). The range of exposures for *Daphnia* was not broad enough to estimate LE_{50} values, but survival was substantially higher in the presence than in the absence of photorepair radiation; all *Daphnia* died in the absence of photorepair radiation (i.e., the $-$PRR treatments) (Fig. 3).
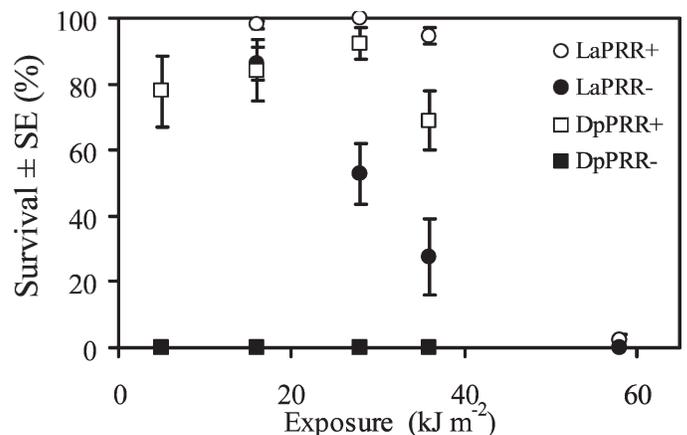

Fig. 3. Survival of *Daphnia pulicaria* (Dp) and *Leptodiaptomus ashlandi* (La) following exposure to UV-B radiation in the presence (PRR+) and absence (PRR$-$) of photorepair radiation in the phototron. Note the reduced survival of *Leptodiaptomus* and total lack of survival of *Daphnia* in the absence of PRR, reflecting the relative importance of PRR in these two species.

Photoprotective compounds—While *Leptodiaptomus* specimens in all lakes were pigmented and orange to red in color, all *Daphnia* were transparent and nonmelanic. *Leptodiaptomus* females contained higher amounts of carotenoids and MAAs than *Daphnia*. In *Leptodiaptomus*, we found 1.9 ± 0.3 μg (mg dry mass)$^{-1}$ carotenoids and a total concentration of 1.46 ± 0.31 μg (mg dry mass)$^{-1}$ MAAs. The concentrations of photoprotective compounds in the *Daphnia* specimens were much lower—carotenoid concentrations of 0.05 ± 0.01 μg (mg dry mass)$^{-1}$ and MAAs of 0.05 ± 0.04 μg (mg dry mass)$^{-1}$.

Discussion

Our results support and extend previous experimental and observational studies on UV and zooplankton by demonstrating a strong relationship ($R^2 = 0.92$–0.95) between UV radiation and the depth distribution of certain zooplankton in alpine lakes, even in the presence of fish and other influencing factors. The vertical distribution of noncalanoid zooplankton was deeper in more UV transparent systems, and this relationship with UV was stronger than that with either food (Chl *a*) or visible light (PAR) (Table 2). The CCA supported this pattern of a strong relationship between UV and zooplankton community structure (Fig. 2). Most striking was the difference in response of the calanoid copepods, which were associated with higher UV environments vs. the noncalanoid zooplankton, which were either associated with high PAR (*Daphnia*) or low PAR (cyclopoids and nauplii). As a consequence of these patterns, calanoids tended to be more deeply distributed in the water column than the other zooplankton in the less UV transparent subalpine lakes and more shallowly distributed in the more UV transparent alpine lakes (Table 1).

These vertical distribution patterns have several important implications for the vertical distribution of zooplankton in transparent lakes. The positive association of *Daphnia* with PAR suggests that visual predation is not likely to be a major factor controlling the distribution of this highly edible and important grazer in alpine and subalpine lakes. This is consistent with the transparency-gradient hypothesis. The shallower distribution of calanoid copepods in the high-UV alpine lakes enables them to exploit the warmer surface waters, while the deeper distribution of the other taxa likely slows metabolism and hence feeding and reproduction due to colder temperatures but puts them closer to the food resources in the DCM. This pattern was particularly pronounced in Fossil Lake, the most UV-transparent system, where peak densities of the calanoids occurred in the high-UV, warmer surface waters ($>12^\circ$C), while peak densities of *Daphnia* and cyclopoids were coincident with the depth of the DCM at 18 m, where temperatures are only 4–5°C (Table 1; Fig. 1). Previous studies have demonstrated a similar demographic sacrifice resulting from a downward migration of zooplankton into colder waters in response to predation (Pangle and Peacor 2006; Pangle et al. 2007). Previous findings have also demonstrated that some copepods prefer higher water temperatures (Johnson et al. 2007), though this was not observed in our study, where the depth of maximum copepod abundance was independent of temperature.

Visual predation is commonly invoked to explain the downward migration of zooplankton during the day (Lampert 1989). However, disentangling the effects of fish predation and UV is very difficult due to the fact that light is the proximate stimulus for both of these factors. Interestingly, in spite of the extensive experimental evidence for UV avoidance (*see* Introduction) and the fact that visual light actually stimulates positive phototaxis in *Daphnia* (Storz and Paul 1998), no prior studies of visual predation have considered the UV avoidance hypothesis. We compared the relative importance of fish predation and UV avoidance in situ by examining the relationship between the vertical distribution of zooplankton and two proxy variables: visible (PAR) transparency as a proxy for visual predation, and short-wavelength UV (320 nm) transparency as a proxy for UV damage avoidance. This was possible because UV and PAR transparencies varied differently among our study lakes.

The stronger response of several zooplankton groups to UV than to PAR observed here supports the transparency-gradient hypothesis, which states that UV is a more important driver than fish predation in more transparent, low-productivity lakes. This is also consistent with prior studies that have shown that fish predation has little or no effect on the vertical distribution of alpine zooplankton (Winder et al. 2004). There are two other lines of evidence that support the contention that fish predation is not likely to explain the vertical distribution patterns observed in our lakes. First, the light intensity at which the zooplankton maxima were observed had sufficient PAR to support high levels of fish predation. The light intensity at which fish larvae can detect zooplankton is optimal around 3000 lux (Richmond et al. 2004), which is equivalent to $\sim$53.6 μmol m^{-2} s^{-1} when using a conversion factor of 0.01786 (Both 2002). The depth of the maximum zooplankton abundance in our study lakes was frequently shallower than the 10% PAR depth (Table 1). Incident midday peak PAR measurements during the sampling period were $\sim$1800 μmol m^{-2} s^{-1}, resulting in light levels at the 10% PAR depth on the order of $\sim$180 μmol m^{-2} s^{-1}, well above the optimum for visual predation. The second line of evidence that suggests that fish predation was not driving these species differences in vertical distribution is that in the less transparent subalpine lakes where fish are abundant, the more-visible and slower-swimming *Daphnia* were generally shallower in their distribution than the calanoids (Table 1).

Several other lines of evidence support the contention that UV is important to the vertical distribution and abundance of zooplankton in alpine lakes. First, underwater UV exposure levels in alpine lakes are high due to a combination of the high levels of incident UV (11% increase in 320 nm UV and a 24% increase in 300 nm UV per 1000 m elevation; Blumthaler et al. 1997) and the high transparency to UV due to low dissolved organic carbon and phytoplankton concentrations (Morris et al. 1995; Laurion et al. 2000; Sommaruga 2001). Even in

lowland lakes, less than a single day of exposure in the surface waters of high-UVR lakes can kill UVR-sensitive zooplankton such as *Daphnia*, while some species of Diaptomid copepods are more UVR tolerant (Williamson et al. 1994; Leech and Williamson 2000). Diaptomid copepods also generally have greater amounts of photoprotective compounds than *Daphnia*, as shown by both the tests of representative species in our study lakes as well as prior studies of photoprotective compounds in copepods and *Daphnia* from around the world (Tartarotti et al. 2001; Persaud et al. 2007). The carotenoid and MAA concentrations that we measured were actually lower than in many of the calanoid copepods in these prior studies, suggesting that the calanoid copepods in our study may also be dependent on photoenzymatic repair. This was supported by our UV lamp phototron experiment, where *L. ashlandi* had significantly higher survival in the presence of photorepair radiation than in its absence.

Some species of calanoids of the family Diaptomidae have been found to actually benefit from moderate levels of UVR exposure (Cooke and Williamson 2006). Previous short-term experiments in microcosms where adult female *Leptodiaptomus ashlandi* were incubated in the surface waters of Beartooth Lake revealed a high level of UVR tolerance in the adults but decreases in reproduction as well as in the survival of the nauplii (Cooke et al. 2006). Thus, some consideration must be given to these more subtle sublethal effects of UV and not to just adult mortality. Southern Hemisphere calanoids in the genus *Boeckella* appear to be more variable in their UV tolerance than Diaptomids (Zagarese et al. 1997; Wubben et al. 2001), though most species of Diaptomids have yet to be tested for their UV tolerance levels. Perhaps some of the most compelling evidence for the importance of UV in controlling zooplankton community structure in alpine lakes is that only a single species of large red copepod persists in systems where the maximum lake depth is less than the 10% $UV_{320\,nm}$ attenuation depth of the lake (Marinone et al. 2006).

There are also several important caveats here due to the potentially complex but very poorly understood relationship between fish and UV transparency. For example, while essentially no data are available on the effects of fish on UV transparency, it has been well established that the presence of fish can have a strong effect on lake transparency to visible light (Mazumder et al. 1990; Parker and Schindler 2006). In alpine lakes, in particular, the removal of stocked salmonids increased Secchi depth from 3.1 to 9.2 m (Parker and Schindler 2006). The second important caveat is that some salmonids have UV vision, though whether or not this is important to feeding in situ is still an open question (Leech and Johnsen 2003). If fish can use longer-wavelength UV to feed, the avoidance of shorter-wavelength UV may help reduce visual predation as well as UV damage.

We suggest that it is time to go beyond the often made assumption that visual predation by fish is the primary driver of diel vertical migration in zooplankton. Just as there is a wide range of trade-offs in zooplankton defenses against UV with taxon and latitude (Hansson et al. 2007), more consideration needs to be given to the more comprehensive transparency-gradient hypothesis to account for differences in drivers of vertical distribution among lakes. Both experimental and in situ evidence now supports the importance of both fish predation and avoidance of UV damage in determining the vertical distribution of zooplankton during the day, where the relative importance of these two variables depends on the transparency of the body of water and strength of fish predation.

References

AGUILERA, X., G. CRESPO, S. DECLERCK, AND L. DE MEESTER. 2006. Diel vertical migration of zooplankton in tropical high mountain lakes (Andes, Bolivia). Pol. J. Ecol. **54:** 453–464.

ALONSO, C., V. E. ROCCO, J. P. BARRIGA, M. A. BATTINI, AND H. E. ZAGARESE. 2004. Surface avoidance by freshwater zooplankton: Field evidence on the role of ultraviolet radiation. Limnol. Oceanogr. **49:** 225–232.

APHA. 1989. Standard methods for the examination of water and wastewater, 17th ed. American Public Health Association.

BLUMTHALER, M., W. AMBACH, AND R. ELLINGER. 1997. Increase in solar UV radiation with altitude. J. Photochem. Photobiol. B **39:** 130–134.

BOEING, W. J., D. M. LEECH, C. E. WILLIAMSON, S. L. COOKE, AND L. TORRES. 2004. Damaging UV radiation and invertebrate predation: Conflicting selective pressures for zooplankton vertical distribution in the water column of low DOC lakes. Oecologia **138:** 603–612.

BOTH, A. J. 2002. Light conversions for plant growth. Horticult. Eng. **3:** 4–7.

COOKE, S. L., AND C. E. WILLIAMSON. 2006. Positive effects of UV radiation on a calanoid copepod in a transparent lake: Do competition, predation or food availability play a role? J. Plankton Res. **28:** 171–179.

———, ———, AND J. E. SAROS. 2006. How do temperature, dissolved organic matter and nutrients influence the response of *Leptodiaptomus ashlandi* to UV radiation in a subalpine lake? Freshwater Biol. **51:** 1827–1837.

DE MEESTER, L. 1993. Genotype, fish-mediated chemicals, and phototactic behavior in *Daphnia magna*. Ecology **74:** 1467–1474.

DODSON, S. I. 1990. Predicting diel vertical migration of zooplankton. Limnol. Oceanogr. **35:** 1195–1200.

FISCHER, J. M., J. L. NICOLAI, C. E. WILLIAMSON, A. D. PERSAUD, AND R. S. LOCKWOOD. 2006. Effects of ultraviolet radiation on diel vertical migration of crustacean zooplankton: An in situ mesocosm experiment. Hydrobiologia **563:** 217–224.

HÄDER, D. P., AND R. P. SINHA. 2005. Solar ultraviolet radiation–induced DNA damage in aquatic organisms: Potential envrionmental impact. Mutat. Res. **571:** 221–233.

HAIRSTON, N. G., JR. 1980. The vertical distribution of diaptomid copepods in relation to body pigmentation, p. 98–110. *In* W. C. Kerfoot [ed.], Evolution and ecology of zooplankton communities. Univ. Press of New England.

HANSSON, L.-A., S. HYLANDER, AND R. SOMMARUGA. 2007. Escape from UV threats in zooplankton: A cocktail of behavior and protective pigmentation. Ecology **88:** 1932–1939.

JOHNSON, C. R., W. J. O'BRIEN, AND S. MACINTYRE. 2007. Vertical and temporal distribution of two copepod species, *Cyclops scutifer* and *Diaptomus pribilofensis*, in 24 h arctic daylight. J. Plankton Res. **29:** 275–289.

KESSLER, K., AND W. LAMPERT. 2004. Fitness optimization of *Daphnia* in a trade-off between food and temperature. Oecologia **140:** 381–387.

LAMPERT, W. 1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. **3:** 21–27.

LAURION, I., M. VENTURA, J. CATALAN, R. PSENNER, AND R. SOMMARUGA. 2000. Attenuation of ultraviolet radiation in mountain lakes: Factors controlling the among- and within-lake variability. Limnol. Oceanogr. **45:** 1274–1288.

LEECH, D. M., AND S. JOHNSEN. 2003. Behavioral responses—UVR avoidance and vision, p. 455–481. *In* E. W. Helbling and H. E. Zagarese [eds.], UV effects in aquatic organisms and ecosystems. Comprehensive series in photochemistry & photobiology. Royal Society of Chemistry.

———, A. PADELETTI, AND C. E. WILLIAMSON. 2005*a*. Zooplankton behavioral responses to solar UV radiation vary within and among lakes. J. Plankton Res. **27:** 461–471.

———, AND ———. 2000. Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? Ecol. Appl. **10:** 1530–1540.

———, AND ———. 2001. In situ exposure to UV radiation alters the depth distribution of *Daphnia*. Limnol. Oceanogr. **46:** 416–420.

———, ———, R. E. MOELLER, AND B. R. HARGREAVES. 2005*b*. Effects of ultraviolet radiation on the seasonal vertical distribution of zooplankton: A database analysis. Archiv Hydrobiol. **162:** 445–464.

MACFADYEN, E. J., C. E. WILLIAMSON, G. GRAD, M. LOWERY, W. H. JEFFREY, AND D. L. MITCHELL. 2004. Molecular response to climate change: Temperature dependence of UV-induced DNA damage and repair in the freshwater crustacean *Daphnia pulicaria*. Glob. Change Biol. **10:** 408–416.

MARINONE, M. C., S. M. MARQUE, D. A. SUÁREZ, M. C. DIÉGUEZ, P. PÉREZ, P. D. LOS RÍOS, D. SOTO, AND H. E. ZAGARESE. 2006. UV radiation as a potential driving force for zooplankton community structure in Patagonian lakes. Photochem. Photobiol. **82:** 962–971.

MAZUMDER, A., W. D. TAYLOR, D. J. MCQUEEN, AND D. R. S. LEAN. 1990. Effects of fish and plankton on lake temperature and mixing depth. Science **247:** 312–315.

MCNAUGHT, A. S., D. W. SCHINDLER, B. R. PARKER, A. J. PAUL, R. S. ANDERSON, D. B. DONALD, AND M. AGBETI. 1999. Restoration of the food web of an alpine lake following fish stocking. Limnol. Oceanogr. **44:** 127–136.

MOELLER, R. E., S. GILROY, C. E. WILLIAMSON, G. GRAD, AND R. SOMMARUGA. 2005. Dietary acquisition of photoprotective compounds (mycosporine-like amino acids, carotenoids) and acclimation to ultraviolet radiation in a freshwater copepod. Limnol. Oceanogr. **50:** 427–439.

MORRIS, D. P., H. E. ZAGARESE, C. E. WILLIAMSON, E. G. BALSEIRO, B. R. HARGREAVES, B. MODENUTTI, R. E. MOELLER, AND C. QUEIMALINOS. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. Limnol. Oceanogr. **40:** 1381–1391.

PANGLE, K. L., AND S. D. PEACOR. 2006. Non-lethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia mendotae*. Freshwater Biol. **51:** 1070–1078.

———, ———, AND O. E. JOHANNSSON. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology **88:** 402–412.

PARKER, B. R., AND D. W. SCHINDLER. 2006. Cascading trophic interactions in an oligotrophic species–poor alpine lake. Ecosystems **9:** 157–166.

PERSAUD, A. D., M. T. ARTS, AND N. D. YAN. 2003. Photoresponses of late instar *Chaoborus punctipennis* larvae to UVR. Aquat. Ecol. **37:** 257–265.

———, R. E. MOELLER, C. E. WILLIAMSON, AND C. W. BURNS. 2007. Photoprotective compounds in weakly and strongly pigmented copepods and co-occurring cladocerans. Freshwater Biol. **52:** 2121–2133.

RHODE, S. C., M. PAWLOWSKI, AND R. TOLLRIAN. 2001. The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. Nature **412:** 69–72.

RICHMOND, H. E., T. T. HRABIK, AND A. F. MENSINGER. 2004. Light intensity, prey detection and foraging mechanisms of age 0 yellow perch. J. Fish Biol. **65:** 195–205.

SAROS, J. E., T. J. MICHEL, S. INTERLANDI, AND A. P. WOLFE. 2005. Resource requirements of *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: Implications for recent phytoplankton community reorganizations. Can. J. Fish. Aquat. Sci. **62:** 1681–1689.

SIEBECK, O., T. VAIL, C. E. WILLIAMSON, R. VETTER, D. HESSEN, H. ZAGARESE, E. LITTLE, E. BALSEIRO, B. MODENUTTI, J. SEVA, AND A. SHUMATE. 1994. Impact of UV-B radiation on zooplankton and fish in pelagic freshwater ecosystems. Archiv Hydrobiol. Beih. Ergebn. Limnol. **43:** 101–114.

SOMMARUGA, R. 2001. The role of solar UV radiation in the ecology of alpine lakes. J. Photochem. Photobiol. B **62:** 35–42.

STORZ, U. C., AND R. J. PAUL. 1998. Phototaxis in water fleas (*Daphnia magna*) is differently influenced by visible and UV light. J. Comp. Physiol. A **183:** 709–717.

TARTAROTTI, B., I. LAURION, AND R. SOMMARUGA. 2001. Large variability in the concentration of mycosporine-like amino acids among zooplankton from lakes located across an altitude gradient. Limnol. Oceanogr. **46:** 1546–1552.

TER BRAAK, C. J. F., AND P. SMILAUER. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination. Microcomputer Power.

WILLIAMSON, C. E., P. J. NEALE, G. GRAD, H. J. DE LANGE, AND B. R. HARGREAVES. 2001*a*. Beneficial and detrimental effects of UV radiation on aquatic organisms: Implications of variation in spectral composition. Ecol. Appl. **11:** 1843–1857.

———, O. G. OLSON, S. E. LOTT, N. D. WALKER, D. R. ENGSTROM, AND B. R. HARGREAVES. 2001*b*. Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. Ecology **82:** 1748–1760.

———, H. E. ZAGARESE, P. C. SCHULZE, B. R. HARGREAVES, AND J. SEVA. 1994. The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. J. Plankton Res. **16:** 205–218.

WINDER, M., P. SPAAK, AND W. M. MOOIJ. 2004. Trade-offs in *Daphnia* habitat selection. Ecology **85:** 2027–2036.

WUBBEN, D. L., E. VARESCHI, I. HAWES, AND G. BODEKER. 2001. Differential UVB-sensitivities of five New Zealand freshwater zooplankton species. N. Zeal. J. Mar. Fresh. Res. **35:** 635–645.

ZAGARESE, H. E., M. FELDMAN, AND C. E. WILLIAMSON. 1997. UV-B–induced damage and photoreactivation in three species of *Boeckella* (Copepoda, Calanoida). J. Plankton Res. **19:** 357–367.

———, AND C. E. WILLIAMSON. 1994. Modeling the impacts of UV-B radiation on ecological interactions in freshwater and marine ecosystems, p. 315–328. *In* R. H. Biggs and M. E. B. Joyner [eds.], Stratospheric ozone depletion/UV-B radiation in the biosphere. NATO ASI Series. Springer-Verlag.